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ON TRANSLOCATION OF CHARACTERS IN PLANTS.

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(Continued from page 19.)

THE SIGNIFICANCE OF THE ABNORMAL FORMS ABOVE DESCRIBED.— Since I hold that the reality of alleged atavism is always to be judged in the light of all related facts in each instance, and that teratological evidence alone is never conclusive, I proceed now to consider whether the abnormal forms described at the beginning of this paper can in view of our present knowledge be regarded as *reversions*, in the modern understanding of the word; and concluding that they cannot be so understood, I shall offer another explanation.

Drosera rotundifolia.— We have seen that certain of the carpels of the deformed flowers have taken on the form and produced the peculiar appendages of foliage leaves with exactness. To assume that this modification constitutes a reversion would be to assume that the foliage leaf of to-day closely conforms to the original from which the present Droseraceous carpel as a distinct organ has descended. But it is safe to say that the carpel of *Drosera* had its origin in common with that of other Angiosperms. It runs back through a series of forms, none of which is a foliage leaf, to the sporophyll of the earliest Angiosperms. Likewise, the foliage leaf of *Drosera* is a derived structure, probably more recent than the family Droseraceae, even. Its peculiarities arose subsequently to the establishment of the Angiospermous, and even the Droseraceous, carpel. It is likely that the differentiation of spore-bearing leaf (sporophyll) and vegetative leaf antedated even the period of the first flowering plants. To reach a point where the vegetative and

reproductive functions were united in a single foliar organ we must probably go back into the fern-like ancestry. The common original of modern Angiospermous foliage leaf and carpel, then, was in all probability a kind of fern frond. The aberrant carpel of *Drosera* bears no resemblance to a fern frond.

It is evident that the abnormal carpel does not reproduce a form from which it has been derived, but rather has taken to itself properties of a coördinate derivative member, the foliage leaf. The abnormal carpel is not, therefore, in any strict sense reversionary. But it may be held that the phenomenon is atavistic in its general tendency. This however is not the case. If we inquire which of the two states, the normal carpellary, or the tentaculiferous vegetative condition, is more original — that is, whether the leaf or the carpel is more like the common sporophyll ancestor — then we shall have to answer that the carpel is the more conservative. In one important respect only, in that it is a free and independent part, is the leaf less modified. In its anatomy, consistency, and shape, neither of the members is much like the probably fern-like original sporophyll. But certainly the leaf with its very peculiar appendages and physiological activities is the more highly specialized. Also it has lost the power which the original sporophyll possessed of forming spores. The carpel retains this important reproductive function and is still capable of doing some assimilatory work. This general estimate of the relative position of the two kinds of organs in the evolutionary scale, which makes the carpel the more primitive, is supported by a recent judgment of Bower's.¹ "The inflorescence, or flower, on this view, though produced later than the vegetative region in the individual life, embodies the more primitive parts, viz., those which bear the sporangia and spores. The vegetative region is in its origin mostly if not wholly, secondary."

In the phylogenetic meaning, then, the monstrous carpels of *Drosera* are not retrogressive; on the contrary the metamorphosis is, in a sense, progressive.

Gentiana crinita.—In Miss Prince's *Gentian*, similarly, the relation of things in evolutionary time is fortunately clear. The fringe of the corolla lobes, being specific, is a late feature. It is supposedly not so old as the generic characters. The carpel on the other hand

¹ *Science*, 20: 532 (1904).

is an ancient structure. When the abnormal carpel puts on the fringe it displays a character not to be found in its own phylogenetic line. Simply the fringe is borrowed. There is no reversion.

Saxifraga virginensis.— It is more difficult to pronounce upon the nature of staminody in Mr. Sears's *Saxifraga*. Petals may well have arisen by the sterilization of stamens. And if so, the replacement of petals by stamens might be considered as a kind of reversion. But the stamen from which the petal of our Polypetalae was derived (if from any) was not Saxifragaceous; and therefore the super-numerary stamens of *S. virginensis* stand for the originals of the petals only in a very general way, at most. Staminody, which as stated above is found in several widely separated families, is of interest chiefly in conjunction with the opposite conversion, viz., that of stamens to petals, an anomaly of very much commoner occurrence. When we consider the two phenomena together it becomes evident that if one of them is in the nature of reversion, the other cannot be. Indeed, to my mind neither of the abnormalities is atavistic. The actual character of the change is, I believe, the same as that which we have seen in the cases of *Drosera* and *Gentiana* just discussed. By anticipation in the development of the flower, characters of one whorl of organs have passed to a lower circle. Staminody and petalody are phenomena merely of replacement.

MORPHIC TRANSLOCATION.— That which has occurred in these three illustrative cases may perhaps best be grasped under the idea of morphic translocation. The essence of the facts I conceive to be this: that structures which historically have been developed in certain parts of the plant body have suddenly made their appearance in other parts. Droseraceous tentacles we may suppose were the product of a long process of evolution, in the course of which originally sessile glands became stalked, and the stalks acquired an internal mechanism securing flexibility and the transmission of stimulus. These highly remarkable organs were developed as parts of the foliage leaf. Now of a sudden they appear upon the sepals, petals and carpels. The fringe of the *Gentian* came into being as a structure of the corolla and possibly plays a part in the economy of the flower. By a jump it now appears upon the carpel.

In the infinite variety of monstrous forms there are many of a different nature from those which have here been the subject of discussion. Oftentimes new patterns and conformations appear for which no

antecedents are to be sought in the normal composition of the plant body. These and other categories of abnormalities are of interest to the student of evolution. It is my purpose to deal here with only one kind of changes, of which I have endeavored to point out the real character. It would be a profitable labor to discover the modes and limits of morphic translocation as exhibited in monstrous forms. At present I shall merely add to this part of my remarks a few words upon the weight of teratological evidence in certain recent discussions of homologies.

CRITICISM OF RECENT ARGUMENTS FROM TERATOLOGICAL PREMISES. — In the egg apparatus of the embryo sac in flowering plants are three cells, of which one is larger than its two neighbors. The large cell is the egg, the smaller ones are the synergids. The egg-cell is held to be the last vestige of an archegonium, the accessory parts of which have been lost — unless the synergids represent the parts. What portions of the original archegonial or prothallial arrangement the synergids represent is wholly obscure. But it has been found that occasionally one of the synergids becomes capable of fertilization, *i. e.*, becomes an egg cell. Some writers have held this exceptional behavior to show that the synergids, as potential egg-cells, are degenerate egg-cells in fact, historically coördinate with the egg proper. Again, in the venter of the archegonium of *Pinus* there are two cells. One is large and destined to be fertilized, the egg. The other, or ventral canal cell, is small and transitory. Rarely, however, the latter cell becomes enlarged and in all visible respects egglike. This abnormality is regarded by Coulter and Chamberlain,¹ as strong evidence in favor of the conclusion that “the ventral canal cell represents an abortive egg, which is occasionally organized as an egg, and which may rarely function as one.” In the cones of the *Abietaceae* the ovuliferous scales have sometimes been found more or less perfectly replaced by leaf-bearing shoots. From this it has been argued² by Braun, Caspary, Parlato, Oersted and others that the fertile scale is morphologically a reduced branch in the axil of the sterile one.

As far as the teratological facts themselves are concerned, without the aid of the more important collateral evidence, these three cases

¹ Seed Plants, p. 87.

² Summary and references in *op. cit.*, ch. III.

are ambiguous. They may or may not be genuine instances of reversion. They are possibly assignable to the category of translocations.

They would, however, be highly suggestive as independent sources of evidence, were it not that it can be clearly demonstrated that organs may be replaced by non-homologous organs, or may combine in themselves along with their own proper characters, the attributes of organs with which they are not homologous. Modifications of the Angiospermous ovule are especially instructive on this point. Masters has assembled¹ in his *Teratology* many accounts, from which it appears that, in addition to the modification described above from Planchon, ovules may be replaced by whole anthers, whole pistils, leaflets, whole leaves, and finally leafy shoots. The fusion of characters may be in any proportion. Thus in *Passiflora coerulea*, Salter² found a complete series of formations connecting anthers and ovules. "The pollen-bearing ovules were borne on the edges of these ovaries, and presented various intermediate conditions between anthers and ovules, commencing at the distal extremity of the carpel with a bilobed anther, and passing in series to the base of the ovary, an antheroid body of ovule-like form, a modified ovule containing pollen, an ovule departing from a perfectly natural condition only in the development of a few grains of pollen in its nucleus, and, finally, a perfect, normal ovule." Similarly Berkeley³ found in a Carnation the characters of ovules and pistils blended in various degrees. Wigand⁴ explicitly states that in *Reseda alba* he observed ovules in all stages of shoot-formation. The conversion of the nucellus to a branch has also been observed in *Alliaria* (*Sisymbrium*) and *Nigrella*. It is plain that whatever the morphology of the ovule, it cannot be the homologue of *all* the structures enumerated above, whose details it occasionally borrows. And these considerations throw much doubt upon the teratological evidence, considered as self-sustained testimony, supposed to reveal the nature of synergid, ventral canal cell, and ovuliferous scale. Before the abnormal formations can be held to be significant in a phylogenetic way, it must be shown that they are not to be classed with these various modifications of the ovule, as phenomena of morphic translocation.

¹ *Vegetable Teratology*, pp. 262-271. ³ *L. c.*, 267.

² *L. c.*, 186. ⁴ *Grundlegung des Pflanzen-Teratologie*, p. 39.

Characters may pass from members of one kind to those of a morphologically different kind. Morphic translocation seems usually to be conditioned not by homology, but by similarity in the developmental substratum. The rudiment of an ovule, which is an emergence of the placental tissue, is much like that of the Droseraceous tentacle; this I can attest from a study of the development of the latter organ. It is also like the beginning of the leaf at the summit of the stem. The partly developed nucellus is a mound of embryonic tissue not unlike the growing stem tip. When vegetative impulses invade the flower the formative forces seize upon the ovular or nucellar rudiments and mould them into vegetative organs, such as are normally produced in the vegetative parts from similar originals. The ovules, or rather their substitutes, then appear as tentacles, leaves, etc., even as whole leaf-bearing shoots.

I have not here discussed the merits of the questions at issue, but have criticized the arguments. However, in the case of the enlarged ventral canal cell, it seems to me that reversion, in any true sense, is extremely unlikely. To find an archegonium-like organ in which more than one gamete was a normal condition, we should have to go back over an enormous stretch of history, certainly to the predecessors of the lowest Hepaticæ, perhaps into the Algæ. I know of no clear indication that characters remain latent for such lengths of evolutionary advance. Characters clearly Pteridophytic do not appear anomalously in Angiosperms, nor Bryophytic anomalies, so far as I am aware, in Ferns. The approximation of the ventral canal cell to the egg in size and structure is probably brought about in the way already suggested: a character which in the course of normal events has been evolved in one member, the egg, has thereby become potential for another member similarly conditioned and of like form in the inceptive stage, and may abnormally become actualized in that other member, the ventral canal cell. *The precedents for monstrosities may thus often be sought in contemporary normal parts, rather than in ancestral conditions.*

MORPHIC TRANSLOCATION IN EVOLUTION. — While organic chaos would result from frequent substitutions occurring in the normal constructive sequence of ontogenetic development and while great translocational capacity would be antagonistic to adequate permanence of type, yet within certain limits the principle might operate without disastrous results and might even, by introducing new combinations

of old characters, contribute to evolutionary progress. But before the translocational property can be admitted as an evolutionary factor it must be shown to be transmissible from generation to generation.

Two of the cases described early in this paper are in point. Mr. Fernald states that he found the variety of *Drosera rotundifolia* which he has called *comosa*,¹ in great abundance, covering the bog where it grew. When a trait is found thus in very numerous individuals it must be entered in the evolutionary account book. The pentadecandrous Saxifrage seems also to be a fixed form. Sterns judged it to be propagated by seed; and Mr. Sears has written me that he has found it — in not a little quantity, as appears from the amount of material sent to me — at a certain station repeatedly since 1886. The experience of gardeners in the propagation of “double” flowered races of plants, in which stamens have turned to petals, is well known. Such forms of Begonia, the Stock, Hollyhock, Columbine, etc., may be raised from the seed. I may also adduce the experiments of De Vries² with an aberrant *Linaria vulgaris*. The flowers were peloric. The spur character had passed from the anterior petal of the gamopetalous corolla to all the other petals and the corolla tube had thus become 5-spurred. In three generations from the seed of peloric plants De Vries found, out of 119 individuals, 106 fully peloric. The form was, therefore, in a high degree, although not fully, true to seed. Changes of organization of the kind here being considered are therefore inheritable, and call for a place in the scheme of evolution.

TRANSLOCATION OF CHARACTERS IN COMPOUND LEAVES, FOLLOWING MODIFICATIONS ARISING IN THE COURSE OF NORMAL EVOLUTION. — With relation to the main theme of this paper I wish now to point out certain aspects of compound leaves. Compounding of the leaf is found in many divisions of Dicotyledons from the most primitive, as Juglandaceae, to the most advanced, as Caprifoliaceae. The compound-leaved groups are separated by entire-leaved allies in such a way that we know compounding to have arisen repeatedly and independently. In families which include some species with entire leaves, others with leaves lobed, parted, etc., and finally some with leaves fully compound, we see, as it were, the compounding in process of development. It is quite certain that this process has been

¹ RHODORA 7:9.

² Die Mutationstheorie 1: 562.

repeated many times, so that by universal consent the compound habit is not regarded as a mark of relationship.

Certain leaf characters are common to entire and to compound leaves, and are widely spread throughout the series. Such are stipules, and absciss-layers of cells at the bases of petioles, causing defoliation. These characters may be considered older than the several cases of compounding.

Certain other characters are found only in compound forms, and since they cannot exist in entire-bladed leaves, must be of later historic development than the cases of compounding where they severally occur. Such features are stipels and absciss-layers of cells in petiolules.

These characters, being later than the compounding which they accompany, are later than the stipules and petiolar absciss-layers of the same species, which features are older than the compounding. Moreover stipels and petiolular absciss-layers occur in widely separated families and must therefore have arisen several times independently in the case of stipels, and many times independently in the case of absciss-layers.

Stipels are found in Staphyleaceae — e. g., *Staphylea trifoliata*, *S. pinnata*, *S. Bumalda*, *Euscaphis staphyleoides*, *Turpinia occidentalis*; in Rutaceae — e. g., *Zanthoxylum carolinianum*, *Z. americanum*; in many Leguminosae (Papilionaceae) — e. g., species of *Phaseolus*, *Robinia*, *Bradburya*, *Desmodium*, *Dolicholus*, *Galactia*, *Vigna*, *Amorpha*; and in Caprifoliaceae — e. g., *Sambucus canadensis* and *S. racemosa*. In looking over these examples one is struck by two general relations. *First*, in all these cases stipels have been preceded by stipules. *Sambucus canadensis* is usually exstipulate it is true, but *S. racemosa* is stipulate, and on young vigorous shoots of *S. canadensis* itself I have found stipules; the stipulate habit is in the genus and occasionally in the species, therefore, I may add that the stipels are by no means constantly present. *Secondly*, in all cases observed there is a close resemblance of stipules and stipels in the same species. Thus in *Staphylea* the stipules are relatively long, linear, pale, and membranaceous; the stipels, though smaller, answer to the same description. In *Turpinia occidentalis* the stipules are much reduced, and the stipels also. In *Zanthoxylum carolinianum* and *americanum* the stipules are spiny and rather stout; the stipels agree. In *Robinia viscosa* and other species of the genus, the stipules are

sharp and rigid; the stipels, though weaker are rigid and sharply pointed. In most other Papilionaceae where both kinds of organs occur the stipules and stipels correspond closely in being slight, filiform structures. In *Sambucus canadensis* the stipels are usually terete — occasionally flat and foliaceous — and capitate, with a small glandular depression at the end; the stipules which I found on vigorous suckers were of the same description.

While we may not be able to determine with certainty whether the present peculiarities of the stipules in these species were taken on before or after the appearance of stipels, yet the way in which the two ranks of members accord in detail as they run the gamut of forms is indicative of some fundamental relation between them. I shall define the nature of a possible or probable relation presently.

As to absciss-layers, it is first to be said that the casting of the leaves of deciduous perennials is an active process, and that the result is achieved by the agency of definite cellular structures. Shortly before the time of defoliation active cell-division begins in the tissue at the base of the petiole, where separation is to take place, and a plate of cells is organized. The middle single layer of the plate finally disintegrates and the leaf drops off (when the fibrous strands break) leaving a clean scar.

If one will examine any compound leaf at the time of leaf-fall, he will probably find that as the petiole is disarticulated from the stem, so the leaflets are disarticulated from the rhachis. Eventually the leaf not only falls off, but falls to pieces. Indeed the leaflets often depart while the leaf stalk and rhachis still stand upon the stem held by the fibrous elements, which are not cut in abscission. As far as my observation goes — and I have examined numerous species and groups, ranging widely both taxonomically and geographically — the casting of leaflets is universal in deciduous, compound-leaved plants.

The appearance of the leaflet scars, when compared with leaf scars, at once suggests that the defoliating process is the same in both cases; and the exact researches of von Mohl¹ leave no doubt on this head. The abjection of leaflets is the same structurally positive process as that of leaves. At the base of the petiolule cell division sets in, resulting in the organization of an absciss-layer.

We see, then, that in the evolution of compound leaves two kinds

¹ Bot. Zeit. 18: 274 (1860).

of structures have arisen bearing a close resemblance to structures previously present. It is to be noted that the secondary features have arisen in situations similar to those in which the antecedent features were already to be found. Stipules arise on the axis of the plant where a leaf is given off; stipels arise on the axis of the branched leaf where a leaflet is given off. Petiolar absciss-layers come at the junction of leaf-stalk and stem; petiolular absciss-layers come at the junction of leaflet-stalk and rhachis.

Furthermore, the secondary features seem to be in the main useless. Certain stipels — as the spinous or glandular kinds — are evidently advantageous, or at least functional. But most stipels are weak affairs for which there is no apparent office. With absciss-layers in petiolules, the probability of inutility is very strong indeed. The dismemberment of the exhausted and now valueless leaf, from which plastic materials have been withdrawn, no longer functionally a leaf but merely the form or frame of a leaf, seems superfluous. While uselessness of apparently unimportant members can perhaps in no case be absolutely proved, yet here the probability of it approximates certainty to such a degree that it may properly become a ground of reasoning. It is plainly within the limits of cogency which must be set in all such arguments as the present, based as they are not upon experiment but only upon observation. I shall assume, then, that for the most part the secondary features in question are useless.

Why have these structures arisen so often, that is repeatedly and independently, in Dicotyledons? And especially why do we find one or both of them present so persistently in spite of inutility? These questions find no answer in the modes of evolution assumed to be the common modes: the formations do not seem to be well accounted for as products of evolution by slow steps under guidance of Natural Selection.

The true account of the structures I believe is that they are repetitions, echoes as it were, of the previously existent parts which they so closely resemble, and that they first made their advent fully formed when the conditions for their production had been matured in the course of the evolution of the leaf. The conditions were the development of a distinct rhachis and petiolule, and the establishment, at their junction, of an allocation of parts very much like the allocation obtaining at the insertion of the petiole upon the stem.

We may say that it is a law of plant building, in certain species, that when a certain arrangement is realized the production of stipule and, eventually, absciss-layer must succeed. When therefore a very similar arrangement is attained in the compound leaf of these species, stipels and absciss-layers follow almost perforce, by the operation of the same structural law of sequence. The repetition of conditions not being perfect, however, the result is not certain in the case of stipels: many compound leaves lack them. But as we have seen, the absciss-layer appears highly constant. The passage of characters from location to location in these instances is comparable to that exhibited by peloric flowers, and by the anomalous forms which stand at the beginning of this paper as a text. Stipels and petiolar absciss-layers, characters of many groups of plants, seem to be effects of a principle which for lack of a better expression I have here called morphic translocation.

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A NEW ARABIS FROM RIMOUSKI COUNTY, QUEBEC.

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ON July 18, 1904, an unfamiliar Arabis was collected by Mr. J. Franklin Collins, and subsequently by the writer on one of the headlands which characterize the south shore of the River St. Lawrence at Bic, Rimouski County, Quebec. The plant, growing with *Cerastium alpinum*, var. *beeringianum*, *Saxifraga caespitosa*, *Woodsia oregana*, and other high-northern or northwestern species, on dry calcareous ledges, was strikingly canescent, and, with its strongly refracted pods and white petals immediately suggested Hornemann's *A. Holboellii* of Greenland, and its numerous Rocky Mountain allies.

A careful study of the Greenland plant and of authentic specimens or the original descriptions of its known American representatives fails, however, to identify the strange Arabis from the St. Lawrence. In general habit it resembles many of these species, but its nearest affinity is perhaps with the Greenland *A. Holboellii* itself, from